A STUDY OF FUNDAMENTAL BARS IN FEATHERS.

OSCAR RIDDLE.

The structure and development of feathers have been studied by many investigators. The pigments of feathers have also been the subject of a very great number of researches. In spite, however, of these numerous studies of feather structures and pigments, we know almost nothing of structural differences between pigmented and non-pigmented areas, and nothing at all of the causes which lead to the orderly and definite distribution of pigment into the often complex color-patterns commonly found in birds. In connection with a research directed to these two points it was thought advisable to make a study of certain *defects* which were known to appear occasionally in feathers. It is a preliminary account of my results in this more restricted field — which, however, proved to be a rather significant one — that is to be found in this paper. The work was undertaken in 1904 under the direction of Professor C. O. Whitman in the zoölogical laboratory of the University of Chicago. It is a pleasure to acknowledge the help, encouragement and criticism which Professor Whitman has given in connection with this work.

At the time I took up the study of the defects under consideration, they had been reported but once, and this report had to do with but a single specimen, a single plumage, and a single defect in each feather. This was an account by R. M. Strong[1] of "A Case of Abnormal Plumage" found in a hybrid pigeon. Dr. Strong described and figured two types of abnormalities, and concurred with Professor Whitman, who had reared the bird, in the opinion that the defects were probably caused by malnutrition during the growth of the juvenal plumage. Besides this case, Professor Whitman had observed these or similar defects in the feathers of several of his birds, and my problem was to learn the extent of their occurrence and to determine their cause. In the course of my studies I have found still other abnormalities —

[1] BIOLOGICAL BULLETIN, November, 1902.

or rather, different forms of the same defect — and I shall first give a description of the nature of the defects, and later consider the question of their extent and cause.

Defects in Adult Morphology. — In the adult expanded feather, I have found five types of defects in structure. In Fig. 1, *a* is shown the first type. There is in this case a sharply defined area extending entirely across the feather-vane, in which there are no, or very few, perfect barbules. A cross-section of the feather at this point would show only shaft and barbs. One such area in the entire length of the feather was one of the types described by Strong. I find, however, an abundance of cases where such areas occur at regular intervals practically throughout the length of the feather. This regularity in the spaces separating the defects, indeed, furnished the clue to the nature of the latter. It will be seen that these areas cross the barbs in such a way as to form almost a right angle with them. The same thing is true of the other types of defects and argues for their standing primarily all for the same thing.

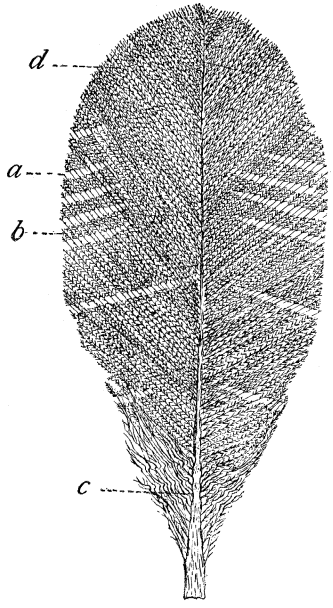

FIG. 1. Feather from a poorly nourished chick showing abnormalities. *a*, abnormal area; *b*, 'fundamental bar' (a day's growth); *c*, constrictions; *d*, region in which defective lines showed plainly in this feather. (× 2.)

The second type represents the greatest extreme to be met with among these abnormalities. The feather in the abnormal region has been reduced to shaft only; both barbules and barbs are gone. The second of the defects described by Strong evidently belonged to this type, though he states that there was no shaft present in his material and that its place was taken by a small cylinder of fused barbs. I have not seen just such a structure as he describes; but it is rare and doubtless is to be regarded as a sort of record of the very severest conditions which

a bird can encounter and endure. In types one and two the barbs and shaft are often bent or kinked in the abnormal region.

The third type of defect is something very much less conspicuous than either of the two types already considered. It could not be represented in the drawing. It is a very minute depression extending across the upper and dorsal surface of the feather. It is not always easy, however, to determine that it is a depression at all. It often seems a line, or simply the point of union of a distal with a proximal part of the feather-vane. This line crosses a series of barbs making with them a right angle as did the defective area of type one. These lines or depressions are usually so inconspicuous that even close observation may not reveal them. Yet they exist and can be demonstrated in all feathers, and at any level throughout the length of the feather.

The existence of these depressions as normal occurrences in the feather is apparently nowhere mentioned in the literature. Certainly their significance has not been made known. As may be inferred from my classification of them, I have found them to bear a close relation to the defective feather areas. These lines which are thoroughly characteristic of feathers are properly classified among feather defects, for, it is always at these lines that the defects like those of types one and four appear and, moreover, they show all possible gradations into types one and four. I shall hereafter speak of defects of this type as *defective lines*, or depressions; those of type one as *defective areas;* those of type four as *constrictions.*

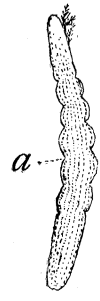

FIG. 2. Entire feather-germ from *Cardinalis virginianus* showing constrictions. (Actual length 13 mm.)

It is those feather-vanes which are made up of a series of deep depressions or constrictions that show the defects of type four. I shall say nothing here of the conditions represented in this type, but perhaps an idea can be had from the feather germ shown in Fig. 2.

Of type five, I have seen but a single example. In this the defect extends vertically or the long way of the feather. The barbs of one half of the vane have their distal portions broken

away at even distances from the shaft. Duerden[1] states that this abnormality is also very rarely met with among ostriches.

The recognition of the defective lines in all feathers throws a new light on abrasion and wear in feathers. That there are birds which "normally" have the barbules broken off at certain fairly definite points in the more distal barbs has been observed by Meves,[2] Chapman,[3] Dwight,[4] Strong[5] and others. Meves and Chapman have noted, too, that the barb itself may be broken near the distal end. I have seen several cases of the breaking of a series of barbs at the point where they were crossed by the same defective line, and I believe that further study will prove that most feather abrasions occur by the space between two defective lines breaking away as a single piece.

The Defects in Feather-germs. — I have been able to observe the defects in several formative stages. I shall say only a word concerning them here. The prominent defects in the unexpanded germ are easily recognized by the unaided eye; sometimes they appear as definite constrictions (*Cardinalis virginianus*, see Fig. 2, *a.*), but very often as points of a different color (rectrices of *Turtur risorius*). A microscopic examination of a region which would develop a defective area shows a reduction of cell-growth and division particularly in the region of the barbules.

Extent and Distribution on the Abnormalities.

In the Bird Groups. — In looking for the cause of the defects one turned naturally to the birds to find whether they were widespread or restricted phenomena. I stated that at the time the present work was begun, there was in the literature but a single account of them, and that account had to do with a single specimen —a hybrid pigeon. Recently Professor J. E. Duerden has

[1] Duerden, "Bars in Ostrich Feathers," *Agr. Jour. Cape of Good Hope*, May 1906.

[2] Meves, W., "Über die Farbenveranderung der Vogel," *Jour. für Ornith.*, Bd. 3, 1855.

[3] Chapman, F. M., "On the Changes of Plumage in the Snowflake," *Amer. Mus. Nat. Hist.*, vol. 8.

[4] Dwight, J., Jr., "The Sequence of Plumages and Moults in the Passerine Birds of New York," *Ann. N. Y. Acad. Sci.*, vol. 13, No. 1.

[5] Strong, R. M., "The Development of Color in the Definitive Feather," *Bull. Mus. Comp. Zool.*, vol. 40, no. 3.

reported the abnormality in the ostriches, particularly in those of South Africa. I learn from him by letter that he has undertaken a thoroughgoing research to determine the cause of the "barring" so prevalent in the ostriches. He estimates that the value of the ostrich plumes from South Africa alone are from this cause depreciated in value to the extent of £250,000 annually.

The defects are, however, not confined to hybrid pigeons and domesticated ostriches. I find them in the most widely separated bird groups; in primitive and in recent birds; in land and in water birds; in domesticated and in wild birds; in birds from the arctic and from the torrid zone, etc. I have been able, owing to the courtesies extended by Professor C. B. Cory and Dr. Ned Dearborn, of the Field Columbian Museum in Chicago, to examine a very great variety of birds belonging to the Museum. I find that although it is not easy to see evident defects in every specimen, it is easy to find them in every species. We may conclude therefore, that they are to be found in *all* birds.

It is a fact, and a significant one I think, that the defects are, in general, more common in domesticated and caged birds than in wild birds. In this connection, however, it should be stated that the defects appear indifferently in pure breeds, hybrids and mongrels. At any rate I have verified this in a number of our domesticated birds.

On Individual Birds. — I have found the defects in all of the plumages of the birds, with the possible exception of the first or downy plumage. In some birds the defects seem to occur more frequently in the juvenal (of Dwight) than in the others. The emphasized defects appear in all the feather-tracts or pterylæ; but in a particular bird, and usually in a particular species, certain tracts show them in greater numbers than do others.

In an Individual Feather. — In the feather there may be produced at any point in its length, either of the five types of abnormality. In some birds (*Gallus*) the distal part of the feather oftener shows the defective *areas;* the proximal end, the deep *constrictions*, while we get defective *lines* in one form or another at every point in the feather's length.

The Meaning and Cause of the Defective Lines and of the Spaces Between Them.

We may now consider the significance of this blocking out of the feather from end to end into bands, "bars," or plane feather-elements, separated from each other by extremely faint depressions or constrictions —for, my studies demonstrate that this is a true conception of feather structure.

That the feather from tip to tip does not represent a perfect, uniform continuity, but is made up of an apposed series of faint "fundamental bars" is a conception which I owe to Professor Whitman. I have proved absolutely that the defective lines, or points of apposition of the "fundamental bars" are the points at which all of the defects appear, and are therefore, really miniature representatives of the defective areas and constrictions of types one and four. I think I have also proved that each block, segment or "fundamental bar" of the feather represents a day of growth, and this is at the same time the amount of feather-growth between two low blood-pressures. Further, I have abundant evidence that the defective lines and areas represent points developed under a diminished rate of cell-growth and cell-division, brought about by a reduced nutrition, which is in turn the result of a daily lowering of the blood-pressure. This low blood-pressure doubtless occurs between one o'clock A. M. and six A. M.

The evidence that a single "fundamental bar" and a single defective line or area are laid down each day, and that this is the total of a day's growth is conclusive. In very favorable material I have been able to show, for example, that a feather 56 days old shows 56 "fundamental bars" and 56 defective lines, areas and constrictions. That the defective area is laid down at night and during a period of low blood-pressure, I have demonstrated twice experimentally. A chick was kept on two succeeding nights, from 8 o'clock P. M. till 8 A. M. in an atmosphere containing amyl nitrite (which lowers the blood-pressure).[1] This bird later showed two emphasized defective areas in the region of the feather produced during the two days of the experiment, and these areas occupied the region normal to the defective lines and

[1] The effect of several drugs on the blood-pressure of birds has been investigated by Dr. S. A. Matthews and the writer. Our results are soon to be published.

did not appear in the territory occupied by a "fundamental bar." Since these defective lines are laid down at approximately the same time each day — as is proved by the regularity in the distances separating them — we are forced to the conclusion that the defective *lines* are normally laid down at night, and that a lowering of the blood-pressure is associated with the production of defective *areas*, and, therefore of defective lines, for, that the defective line stands for the initial stage of the defective area is as certain as that an area has more dimensions than a line. The evidence in part is, that one sees all possible intergradations, that each marks off a day's growth, that when the area occurs it always falls in the place for the line, that a certain part of the line only may be transformed into the obviously defective area, etc. That there is a reduction of cell-growth and cell-division in the defective area is proved absolutely by an examination of the adult morphology of an exaggerated defect, as it is also by the histology of the defects in the feather-germ.

That the low blood-pressure occurs at night is evidenced by the experiment of the chick in the amyl nitrite. That it occurs between midnight and six in the morning may be inferred from the fact that the lowest daily *temperature* in birds falls between these hours. Reasoning from the facts known in mammals we may assume that the minimum blood-pressure coincides in point of time with the minimum temperature. I have not been able to get the daily blood-pressure curve of birds, owing to the difficulty of doing so in birds of small size. The ostriches might well be used for that purpose. At this point I may suggest that the ostriches will doubtless cease to interpolate defective *areas* in their plumes as soon as they can find the perfect diet, and the various life conditions which will give them *well-nourished bodies* and strong, *effective circulations*. After all, these two are one.

The Relation of Nutrition to the Defects.

At the very beginning of this study, it was thought that the defective areas stood in a certain relation to a faulty nutrition. A number of experiments were made to determine this. A number of young ring doves were alternately starved and fed, with the result that in these birds the defective areas appeared in the

juvenal plumage in great numbers. The same experiment was tried on young chicks with the same result. It was noticed, however, that notwithstanding the careful and plentiful feeding of the control, an occasional defect could be found in their feathers too. These experiments[1] showed that malnutrition is beyond doubt the important factor in the production of the defective areas, but apparently not the only one. An experiment was then carried through to learn whether the defects found in the control could be produced by the usual *handling* of the birds, and perhaps slightly crumpling their feather-germs. The results were negative; but it was found that when the feather-germs were *strongly crumpled* and broken in the region of feather growth, the defects were readily produced.

During the progress of an experiment on some young chicks (carried on for a quite different purpose) it was found that chicks which were fed on the fat stain Sudan III produced the defective areas in much greater numbers than did the control birds. It was determined that the ordinary variations of light, temperature, etc., did not cause the defects. The net result so far of all the experiments for the determination of the cause of the defects, indicated that those things which interfere with the *nutrition* of the feather-germ will produce the defects, while those things not capable of affecting the nutrition will not produce them. It is easy to understand how a crumpling of the feather-germ would temporarily interfere with the circulation within it. In the chicks fed with Sudan III. it was evident that a sort of "starving" effect was produced by it. By the time the experiments had proceeded thus far I knew that a day of normal growth in a feather is represented by a "fundamental bar" and a defective line, and also that a defective line stands in close relation to a defective area. This suggested that the defective areas in the control, and the defective lines in all feathers, are produced by an internal factor with a definite rhythm, and that the rhythm is able, like my experiments, to effect the nutrition of the feather elements. This recommended blood-pressure to me, and the experiments were made with the result stated above.

Blood-Pressure and Temperature Rhythms. — I shall not here

[1] Partial results of these feeding experiments were communicated by letter to Professor Duerden and were published in his paper, cited elsewhere.

attempt to explain the causes for the nightly fall of the blood-pressure in birds. Let it suffice to say that we find a parallel phenomenon in mammals. I wish further to call attention to the fact that my demonstration that the lowest blood-pressure in birds falls at night is evidence that the blood-pressure and temperature curves of birds are similar curves, as they are known to be in mammals. Of course, I have not showed a blood-pressure *curve* for birds; I have, however, located in a general way the *time* of its *minimum*. I am in a position to confirm the observations of Corin and Van Beneden[1] as to the temperature curves of birds. They worked with pigeons. I have temperature curves essentially similar to theirs, from ducks, ring-doves, and from chicks both old and young. The lowest temperature occurs at about four to five o'clock A. M.

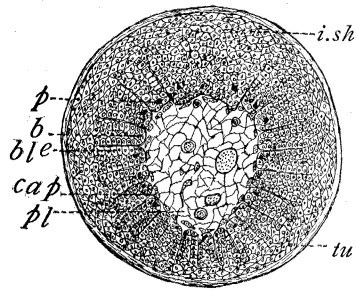

FIG. 3. Cross-section of a fea hergerm in the region of growth. (Semi-diagrammatic, magnified about 100 diameters.) *b*, barb-forming cells; *ble*, barbule-forming cells; *p*, pigment cell; *cap*, capillaries; *pl*, pulp; *tu*, outer sheath; *i.sh*, inner sheath.

Low Blood-Pressure and the Nutrition of the Feather Elements.— There remains to be indicated some of the histological relations of the capillaries and the feather-elements which suffer from the lowering of the vascular tension. I shall also outline the way in which the low pressure probably acts.

Just as among the vertebrates we know that certain tissues, *e. g.*, the liver cells, are kept always on the verge of asphyxiation, so I believe are the epidermal cells of the growing feather-germ taxed to their utmost to secure from the blood enough nourishment to allow the rapid cell-division to proceed in full swing. Where else in an adult vertebrate do we find a more rapid growth and differentiation of tissue than we find in the moulting of certain birds? We may then expect to find here a struggle for food when this becomes reduced in amount, and those parts nearer the blood-supply should fare better than parts

[1] Corin, G., and Van Beneden, A., "La Régulation de la tempérarure chez les Pigeons," *Archives de Biologie*, Vol. VII., pp. 265–276, 1887.

more removed. Now this is exactly what happens. The capillaries (Fig. 3 *cap*) of the feather-germ lie nearest those cells which enter into the formation of the *barbs* (Fig. 3, *b*) and these are able to continue to grow even with a weakened food-supply; they too, though, are suppressed in cases of extreme starvation. The cells which form the *barbules* (Fig. 3, *b*) are not in contact with capillary walls, and can utilize only the surplus of food which filters through the barb-forming cells. With this fact in mind it is clear that we should expect a diminished food-supply to first check the growth in the barbules and that still further reduction is necessary to check the growth of the barbs. Experience proves that this is true (I use the words "food" and "nutriment" in a broad sense, and *oxygen* is to be read into them). It is conceivable that a reduced oxygen-supply is here playing a part, since in all my experiments and in any normal lowering of the blood-pressure, the available oxygen is decreased.

From what has just been said of the filtration method by which the barbule cells receive their nutriment, we can now see how it is that blood-pressure plays so important a part in the production of defective areas. It is well known that when a period of low blood-pressure sets in, the lymph begins to flow from the spaces between the cells of the body into the capillaries. Thus, by withdrawing a quantity of food from the immediate environs of the cell, a low blood-pressure affects the cell in the same way as does an actual reduction of the amount of nourishment circulating in the blood.

It appears, therefore, that the feather germ as it grows and unfolds, spreads before us a record of some earlier significant occurrences within. Indeed, it now seems certain that the delicate filaments, so admirably interlaced to form a feather-vane, are as capable as a revolving drum of recording the important changes in vascular pressure. To be sure, the tracings on the plumes are not to be measured as symmetrical curves with a definite number of millimeters of daily variation, but are written in "fundamental bars" separated by areas more or less imperfect which are to be read in terms of cell-growth and cell-division.

HULL ZOÖLOGICAL LABORATORY,
UNIVERSITY OF CHICAGO,
December, 1906.